# BIODIVERSITY, DEFINITION OF

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## GLOSSARY

**biodiversity/biological diversity** Species, genetic, and ecosystem diversity in an area, sometimes including associated abiotic components such as landscape features, drainage systems, and climate.

**diversity indices** Measures that describe the different components of biodiversity, such as species richness (alpha diversity), beta and gamma diversity, endemicity, and higher taxon richness.

**ecosystem diversity** Diversity of habitats, ecosystems, and the accompanying ecological processes that maintain them.

**endemicity** State of a species or other taxon being restricted to a given area, such as a specific habitat, region, or continent.

**flagship species** Charismatic or well-known species that is associated with a given habitat or ecosystem and that may increase awareness of the need for conservation action.

**genetic diversity** Genetic variety found within or among species; this diversity allows the population or species to adapt and evolve in response to changing environments and natural selection pressures.

**keystone species** Species that has a disproportionately greater effect on the ecological processes of an ecosystem, and whose loss would result in significantly greater consequences for other species and biotic interactions.

**organismal (species) diversity** Number and relative abundance of all species living in a given area.

**species richness** Absolute number of species living in a given area (also called alpha diversity), giving equal weight to all resident species.

**use values** Values that are obtained by using a natural resource, such as timber, fuelwood, water, and landscapes. These include direct, indirect, option, and nonuse values.

*THE WORD BIODIVERSITY IS A MODERN CONTRACTION OF THE TERM BIOLOGICAL DIVERSITY.* *Diversity* refers to the range of variation or variety or differences among some set of attributes; *biological* diversity thus refers to variety within the living world or among and between living organisms.

## I. WHAT IS BIODIVERSITY?

The term "biodiversity" was first used in its long version (biological diversity) by Lovejoy (1980) and is most commonly used to describe the number of species. Recognizing that conventional methods of determining, and separating, species were inadequate, others elaborated the definition by including the variety and variability of living organisms.

These reduced and simple definitions, which embrace many different parameters, have been much elaborated and debated in the last three decades (see Section II); upon this definition hangs the outcome of important scientific considerations, international agreements, conventions, conservation initiatives, political debates, and socio-economic issues. Indeed, while the word "biodiversity" has become synonymous with life on earth, the term is commonly used in the fields of politics and environmental technology in addition to various scientific disciplines (Ghilarov, 1996). The U.S. Strategy Conference on Biological Diversity (1981) and the National Forum on Biodiversity (1986) in Washington, D.C., were the critical debates in crafting a definition, and it was the proceedings from the latter, edited by E. O. Wilson, that "launched the word 'biodiversity' into general use" (Harper and Hawksworth, 1994).

In measuring biodiversity, it is necessary to deconstruct some of the separate elements of which biodiversity is composed. It has become widespread practice to define biodiversity in terms of *genes, species, and ecosystems,* for example, "the abundance, variety, and genetic constitution of native animals and plants" (Dodson *et al.,* 1998). Biodiversity also encompasses all five living kingdoms, including fungi. However, biodiversity does not have a universally agreed on definition and it is often re-defined on each occasion according to the context and purpose of the author.

## II. DEFINITION OF BIODIVERSITY

"Biodiversity" is a relatively new compound word, but biological diversity (when referring to the number of species) is not. Over the last decade its definition has taken a more reductionist turn. Possibly the simplest definition for biodiversity, lacking in specificity or context, is merely the number of species. Yet many have argued that biodiversity does not equate to the number of species in an area. The term for this measure is species richness (Fiedler and Jain, 1992), which is only one component of biodiversity. Biodiversity is also more than species diversity (simply called diversity by some authors), which has been defined as the number of species in an area and their relative abundance (Pielou, 1977).

DeLong (1996) offered a more comprehensive definition:

> Biodiversity is an attribute of an area and specifically refers to the variety within and among living organisms, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans. Biodiversity can be measured in terms of genetic diversity and the identity and number of different types of species, assemblages of species, biotic communities, and biotic processes, and the amount (e.g., abundance, biomass, cover, rate) and structure of each. It can be observed and measured at any spatial scale ranging from microsites and habitat patches to the entire biosphere.

This definition allows for modification according to the context in which it is used.

Various authors have proposed specific and detailed elaborations of this definition. Gaston and Spicer (1998) proposed a three-fold definition of "biodiversity"—ecological diversity, genetic diversity, and organismal diversity—while others conjoined the genetic and organismal components, leaving genetic diversity and ecological diversity as the principal components. These latter two elements can be linked to the two major "practical" value systems of direct use/genetics and indirect use/ecological described by Gaston and Spicer (1998). Other workers have emphasized a hierarchical approach or hierarchies of life systems.

In contrast, some argue that biodiversity, according to the definition of biological, does not include the diversity of abiotic components and processes, and that it is inaccurate to identify ecological processes, ecosystems, ecological complexes, and landscapes as components of biodiversity. The term ecological, as used in the sense of ecological system (ecosystem), encompasses both biotic and abiotic components and processes. Therefore, ecological diversity is a more appropriate term for definitions that include the diversity of ecological processes and ecosystems. However, ecological processes, it has been argued, should be included in the definition of biodiversity, the reasoning being that "although ecological processes are as much abiotic as biotic, they are crucial to maintaining biodiversity." Similarly, a U.S. Bureau of Land Management advisory group included ecological processes in their definition of biodiversity in response to criticism that the Office of Technology Assessment's (1987) definition did not consider ecosystem form and function. Other writers point out that even though ecological processes are often cited as being crucial to maintaining biodiversity (Reid and Miller, 1989; Noss and Cooperrider, 1994; Samson and Knopf, 1994), this does not warrant the inclusion of ecological processes into the meaning of biodiversity. For example, Reid and Miller (1989) and Agarwal (1992) distinguished between biodiversity and the processes and ecological diversity that maintain it.

Nevertheless, the jargon word "biodiversity" is, by its very origin, fundamentally indefinable, being a populist word invented for convenience. Its invention has had beneficial effects by fuelling research projects, mainly in ecology and systematics, and scientists have been drawn into contributing to the debate by the need to show that biodiversity is useful to humans and necessary for the proper functioning of ecosystems. Conservation (i.e., management) of biodiversity is axiomatic to these two concerns and lies behind the scientific need to define the term within whatever context is appropriate, since no general definition will be suitable when applied across a range of situations.

Biodiversity conservation requires the management of natural resources, and this in turn requires the measurement of these resources. Biodiversity measurement implies the need for some quantitative value that can be ascribed to the various measurements so these values can be compared. Among the first scientists to measure diversity were Fisher, Corbet, and Williams (1943), who approximated the frequency distribution of the species represented by 1,2,3,4. . . (and so on) individuals by the logarithmic series $\alpha x$, $\alpha x^2/2$, $\alpha x^3/3$, $\alpha x^4/4$. . . , where the constant $\alpha$ has been found to be a measure of species diversity. Species diversity is low when the number of species is growing slowly with respect to the increase in number of individuals, and it is high when the number of species is growing quickly.

If the need to quantify biodiversity drives the fundamental meaning of biodiversity, the definition may be limited to that which can be readily measured given current understanding and technologies. Such a definition of biodiversity could change over time as ideas, technology, and resources for measuring diversity change. DeLong (1996) suggested that an operational "clause" should be added to the definition of biodiversity, namely, that "biodiversity is. . .as measured in terms of. . . ." This approach provides a link to management while distinguishing between what biodiversity is (a state or attribute) and how it is measured. It also allows the operational clause to be adjusted over time without changing the fundamental meaning of the term. A definition of biodiversity should portray the full scope of what the term means, not just what can be measured and managed. In contrast, monitoring or management objectives must be attainable to be effective. Recognizing the distinction between a definition and management objectives should reduce the confusion between the meaning of biodiversity and the objectives for achieving biodiversity goals.

Biodiversity is a broad totality and often embraces elements beyond species diversity or numbers. For example, a major debate in biological sciences over many decades has been that of pattern versus process, especially in systematics and evolutionary studies. Molecular biology and systematics have enabled ecologists to see that inferred history is important in framing appropriate questions, and this understanding has precipitated a real integration of these twin hierarchies—pattern (e.g., diversity) and process (e.g., evolution). Fundamental divisions remain, such as "straight" parsimony (i.e., pattern) versus maximum likelihood (i.e., process) in the phylogenetic interpretation of sequence data.

It is apparent that the term biodiversity still lacks consistent meaning within the field of natural resource management. Michael Soulé found it shocking that "we are still trying to define biological diversity after all of the efforts of the Office of Technology Assessment and E. O. Wilson's book, *Biodiversity*" (Hudson, 1991). It is still defined in different ways by different people; some characterize biodiversity as being a widely used term "having no unified definition" and others emphasize or limit the meaning of biodiversity to that of native biodiversity. Some writers have included human alterations of biological communities in the scope of biodiversity (Bryant and Barber, 1994). Angermeier (1994) argued that "the absence of a 'native' criterion within the definition [of biodiversity] severely compromises biodiversity's utility as a meaningful biological concept," reasoning that native biodiversity is more valuable than artificial diversity and should be the primary focus of conservation efforts. The conservation of native biodiversity appears to be the theme of biodiversity conservation texts (Wilson and Peter, 1988; Hunter, 1996). Conversely, others argued that an important component of biodiversity is maintained by traditional farming techniques. In the context of conserving biodiversity, Reid and Miller (1989) and Bryant and Barber (1994) discussed the importance of genetic diversity within species of cultivated plants. Biodiversity within agricultural plants is important for pest management in agroecosystems and sustainable agriculture.

An accepted fundamental definition of biodiversity is needed for conservation planning, as are effective communication and co-operation within and among different countries, governments, agencies, disciplines, organizations, and private landowners. Co-operation among these entities has been identified as being necessary for the conservation of biodiversity (Babbitt, 1994). Knopf (1992) asserted that the definitions of biodiversity are "as diverse as the biological resource." Definitions of biodiversity range in scope from "the number of different species occurring in some location" to "all of the diversity and variability in nature" and "the variety of life and its processes." A more comprehensive definition is "the variety of living organisms, the genetic differences among them, the communities and ecosystems in which they occur, and the ecological and evolutionary processes that keep them functioning, yet ever changing and adapting" (Noss and Cooperrider, 1994).

This plethora of terms and definitions is one of the major stumbling blocks to reaching agreement in problem solving and decision making. If entities in a planning process view biodiversity in fundamentally different ways, agreement on management objectives and strategies for biodiversity conservation will be impaired. (Swingland, 1999).

The differences between these conceptual perspectives on the meaning of biodiversity, and the associated semantic problems, are not trivial. Management intended to maintain one facet of biodiversity will not necessarily maintain another. For example, a timber extraction program that is designed to conserve biodiversity in the sense of site species richness may well reduce biodiversity measured as genetic variation within the tree species harvested. Clearly, the maintenance of different facets of biodiversity will require different management strategies and resources, and will meet different human needs.

Even if complete knowledge of particular areas could be assumed, and standard definitions of diversity are derived, the ranking of such areas in terms of their importance with respect to biological diversity remains problematic. Much depends on the scale that is being used. Thus, the question of what contribution a given area makes to *global* biological diversity is very different from the question of what contribution it makes to local, national, or regional biological diversity. This is because, even using a relatively simplified measure, any given area contributes to biological diversity in at least three different ways—through its richness in numbers of species, through the endemism (or geographical uniqueness) of these species (e.g., Mittermeier *et al.*, 1992), and on the basis of degree of threat. The relative importance of these three factors will inevitably change at different geographical scales, and sites of high regional importance may have little significance at a global level. None of these factors includes any explicit assessment of genetic diversity.

Although the word biodiversity has already gained wide currency in the absence of a clear and unique meaning, greater precision will be required of its users if policy and programs are to be more effectively defined in the future.

## III. GENETIC DIVERSITY

Genetic diversity is reliant on the heritable variation within and between populations of organisms. New genetic variation arises in individuals by gene and chromosome mutations, and in organisms with sexual reproduction it can be spread through the population by recombination. It has been estimated that in humans and fruit flies alike, the number of possible combinations of different forms of each gene sequence exceeds the number of atoms in the universe. Other kinds of genetic diversity can be identified at all levels of organization, including the amount of DNA per cell and chromosome structure and number. Selection acts on this pool of genetic variation present within an interbreeding population. Differential survival results in changes of the frequency of genes within this pool, and this is equivalent to population evolution. Genetic variation enables both natural evolutionary change and artificial selective breeding to occur (Thomas, 1992).

Only a small fraction ($<1\%$) of the genetic material of higher organisms is outwardly expressed in the form and function of the organism; the purpose of the remaining DNA and the significance of any variation within it are unclear (Thomas, 1992). Each of the estimated $10^9$ different genes distributed across the world's biota does not make an identical contribution to overall genetic diversity. In particular, those genes that control fundamental biochemical processes are strongly conserved across different taxa and generally show little variation, although such variation that does exist may exert a strong effect on the viability of the organism; the converse is true of other genes. A large amount of molecular variation in the mammalian immune system, for example, is possible on the basis of a small number of inherited genes (Thomas, 1992).

## IV. SPECIES DIVERSITY

Historically, species are the fundamental descriptive units of the living world and this is why biodiversity is very commonly, and incorrectly, used as a synonym of *species diversity,* in particular of "species richness," which is the number of species in a site or habitat. Discussion of global biodiversity is typically presented in terms of global numbers of species in different taxonomic groups. An estimated 1.7 million species have been described to date; estimates for the total number of species existing on earth at present vary from 5 million to nearly 100 million. A conservative working estimate suggests there might be around 12.5 million.

When considering species numbers alone, life on earth appears to consist mostly of insects and microorganisms. The species level is generally regarded as the most natural one at which to consider whole-organism diversity. While species are also the primary focus of evolutionary mechanisms, and the origination and extinction of species are the principal agents in governing biological diversity, species cannot be recognized and enumerated by systematists with total precision. The concept of what a species is differs considerably among groups of organisms. It is for this reason, among others, that species diversity alone is not a satisfactory basis on which to define biodiversity.

Another reason why a straightforward count of the number of species provides only a partial indication of biological diversity concerns the concept of degree or extent of variation that is implicit within the term biodiversity. By definition, organisms that differ widely from each other in some respect contribute more to overall diversity than those that are very similar. The greater the interspecific differences (e.g., by an isolated position within the taxonomic hierarchy), then the greater contribution to any overall measure of global biological diversity. Thus, the two species of Tuatara (genus *Sphenodon*) in New Zealand, which are the only extant members of the reptile order Rhynchocephalia, are more important in this sense than members of some highly species-rich family of lizards. A site with many different higher taxa present can be said to possess more *taxonomic diversity* than another site with fewer higher taxa but many more species. Marine habitats frequently have more different phyla but fewer species than terrestrial habitats, that is, higher taxonomic diversity but lower species diversity. By this measure, the Bunaken reef off the north coast of Sulawesi has the highest biodiversity on earth. Current work is attempting to incorporate quantification of the evolutionary uniqueness of species into species-based measures of biodiversity.

The ecological importance of a species can have a direct effect on community structure, and thus on overall biological diversity. For example, a species of tropical rain forest tree that supports an endemic invertebrate fauna of a hundred species makes a greater contribution to the maintenance of global biological diversity than does a European alpine plant that may have no other species wholly dependent on it.

## V. ECOSYSTEM DIVERSITY

While it is possible to define what is in principle meant by genetic and species diversity, it is difficult to make a quantitative assessment of diversity at the ecosystem, habitat, or community level. There is no unique definition or classification of ecosystems at the global level, and it is difficult in practice to assess ecosystem diversity other than on a local or regional basis, and then only largely in terms of vegetation. Ecosystems are further divorced from genes and species in that they explicitly include abiotic components, being partly determined by soil/parent material and climate.

To get around this difficulty, ecosystem diversity is often evaluated through measures of the diversity of the component species. This may involve assessment of the relative abundance of different species as well as consideration of the types of species. The more that species are equally abundant, then the more diverse that area or habitat. Weight is given to the numbers of species in different size classes, at different trophic levels, or in different taxonomic groups. Thus a hypothetical ecosystem consisting only of several plant species would be less diverse than one with the same number of species but that included animal herbivores and predators. Because different weightings can be given to these different factors when estimating the diversity of particular areas, there is no one authoritative index for measuring ecosystem diversity. This obviously has important implications for the conservation ranking of different areas. In examining beta diversity (i.e., the change in species composition between areas), the only reliable predictor of community similarity is to compare the species composition of the site immediately adjacent.

## VI. BIODIVERSITY: MEANING AND MEASUREMENT

### A. Species Diversity

A. S. Corbet, upon analyzing a large collection of butterflies from Malaya, remarked on the decrease in number of new species with an increasing number of individuals. He thought that the resulting distribution could be described by a hyperbola, but R. A. Fisher, to whom Corbet sent his results, suggested that a negative binomial distribution would be much more appropriate

(Williams, 1964). As mentioned earlier, Fisher, Corbet, and Williams (1943) approximated the frequency distribution of the species represented by 1,2,3,4. . . (and so on) individuals by the logarithmic series $\alpha x$, $\alpha x^2/2$, $\alpha x^3/3$, $\alpha x^4/4$. . . , where the constant $\alpha$ is a measure of species diversity. Species diversity is low when the number of species rises slowly with an increase in the number of individuals, and diversity is high when the number of species rises quickly.

Species diversity measurement was thus clearly formulated more than 50 years ago and a particular index was proposed. Fisher *et al.* attempted to find some general "rule" or "law" according to which the numerical abundances of different species were related to each other. In many communities, the number of species with given abundance could be approximated by the log-normal distribution. If species are classified in accordance with their abundance in logarithmically increasing classes—so-called "octaves" (i.e., the first octave contains 1–2 individuals, the second contains 2–4 individuals, the third has 4–8, the fourth has 8–16, and so on)—then the number of species per "octave" shows a truncated normal distribution. If a sample contains a high number of species and individuals, we can usually obtain a log-normal distribution, and it is obviously more tractable than the logarithmic series.

MacArthur (1957) went further by proposing an interesting model that assumed that boundaries between niches in resource–niche hypervolume are set at random, whereas the relative abundances of species are proportional to these sections of hypervolume. This model became widely known as the "broken-stick" or MacArthur's model. The distribution of abundance prescribed by MacArthur's model is much "flatter" (i.e., the contrast between given species and the next in the sequence is less) than in the case of a logarithmic series (Ghilarov, 1996).

It has become clear that there is no universal type of distribution of relative abundance that corresponds to all real communities, though such distributions change in the course of succession according to a particular pattern. The dominance of a few of the most abundant species is more pronounced at the early stages of succession, while later the species of intermediate abundance become more significant (Whittaker, 1972). A comprehensive understanding of the underlying mechanisms that result in a given pattern of species abundance still eludes scientists.

Another line of species diversity studies was connected with the use of special indices proposed to measure diversity without reference to some hypothetical distribution of relative abundance. A great variety of indices were proposed that assess the number of species and the proportions in abundance of different species. Among others, there was the very popular index that is based on Shannon's formula derived from information theory:

$$H = \Sigma\, p_i \log p_i$$

where $p_i$ is the proportion of the total number of individuals that belong to the $i$th species.

In a seminal work on the measurement of diversity, Whittaker (1972) introduced the concepts of alpha, beta, and gamma diversity. The measurements just described, giving diversity values for single sites, are examples of alpha diversity. The beta and gamma diversity concepts relate to changes in diversity between sites at local (beta) and geographical (gamma) scales. An essential part of these relational concepts is the idea of species turnover—the degree to which species replace other species at different sites. For use in assessing the relative value of multiple sites for the conservation of biodiversity, the idea of species turnover is translated into the principle of complementarity (see Section VIII,A), which can be implemented in combination with a taxonomic diversity index.

## B. Taxonomic Diversity

Biodiversity measurements that measure genetic difference directly, or indirectly through use of the taxonomic (cladistic) hierarchy (Williams *et al.,* 1991), are currently being used. The indirect taxonomic approach is more practical because we already have a "rule of thumb" taxonomic hierarchy (which is being steadily improved through the application of cladistic analysis, notably to molecular data), whereas reliable estimates of overall genetic differences between taxa are virtually non-existent (abridged from Vane-Wright, 1992).

Based on the shared and unshared nodes between taxa (equivalent to position in the taxonomic hierarchy), a number of taxonomic diversity indices have now been developed. Of these, the most distinct are root weight, higher taxon richness, and taxonomic dispersion. The first places highest individual value on taxa that separate closest to the root of the cladogram and comprise only one or relatively few species; in effect this gives high weighting to relict groups (Vane-Wright, 1996). Higher taxon richness favors taxa according to their rank and number of included species. Dispersion, the most complex of the measures proposed so far (Williams *et al.,* 1991), endeavors to select an even spread of taxa across the hierarchy, sampling a mixture of high, low, and intermediate ranking groups.

For a given group these measures, together with simple species richness if desired, can be used to compare the biotic diversity of any number of sites. The measures can also be expressed as percentages. Thus a site with viable populations of all species in a group would have a diversity score of 100%, whereas a site without any species of the group in question would score zero. In reality, of course, most sites have only a selection of species, and so receive various intermediate scores. Such assessments allow us to compare all sites with each other, and rank them individually from highest to lowest diversity (Vane-Wright, 1996). However, if we then take some conservation action (such as conserving a particular site), the same measures are unlikely to be directly comparable for making a second decision (such as choosing a second conservation site). This is because, in most real situations at least, there will be considerable overlap in the presence of species at particular sites.

### C. Community Diversity

Early ecologists did not confine themselves to measuring species diversity. They also tried to understand the relationship of diversity with other features of the community (e.g., Williams, 1964; Whittaker, 1972). The dependence of species diversity on the structural complexity of the environment was demonstrated (MacArthur and MacArthur, 1961), as was the role of predation (Addicott, 1974) and periodical disturbance (Sousa, 1979) in determining a given level of diversity. The relationship between the species diversity and standing crop of a community was also shown (Ghilarov and Timonin, 1972).

Margalef (1957) was the first to use the Shannon index (though expressed in a different form). He proposed to evaluate the level of community organization in terms of information theory. Margalef stimulated many ecologists to quantitatively measure the species diversity of different communities and/or of the same community in different stages of its development. At that time, there was a widespread belief that with a single numerical value, an assessment could be made of some very significant feature of community structure. Many ecologists believed that in measuring species diversity at the community level they were using an approach that was fundamental to an understanding of diversity (Ghilarov, 1996).

Ecologists have measured diversity either by estimating species richness (number of species) in an area, or by using one or more indices combining species richness and relative abundance within an area. Some attempts have also been made to measure change in species richness (species turnover) between areas. These solutions to the problem of measuring biodiversity are limited because species richness takes no account of the differences between species in relation to their place in the natural hierarchy. Moreover, relative abundance is not a fixed property of a species, for it varies widely from time to time and place to place. In many environments most taxa are virtually or even completely unknown.

Conservation biologists, or applied ecologists, have called for a measurement of diversity that is more clearly related to overall genetic difference. An example concerns the problem of differential extinction. In *World Conservation Strategy* (IUCN/UNEP/WWF, 1980), it is noted that "the size of the potential genetic loss is related to the taxonomic hierarchy because. . .different positions in this hierarchy reflect greater or lesser degrees of genetic difference. . . . The current taxonomic hierarchy provides the only convenient rule of thumb for determining the relative size of a potential loss of genetic material."

### D. Synthesis

A model incorporating island biogeographic theory, species abundance, and speciation, and that produces a fundamental biodiversity number ($\theta$) that is closely associated with species richness and abundance in an equilibrium meta-population, has been proposed in Hubbell's unified theory (1997). This model assumes zerosum community dynamics or a saturated, totally stochastic local community, which limits its application, but it advances the study of species richness and relative abundance if others can extend its usefulness to the nonequilibrium systems that characterize the real world.

## VII. BIODIVERSITY: CHANGES IN TIME AND SPACE

### A. Changes Over Time

The fossil record is very incomplete, which emphasizes the marked variation between higher taxa and between species in different ecosystems in the extent to which individuals are susceptible to preservation and subsequent discovery. Chance discovery has played a large part in compiling the known fossil record, and interpretation by paleontologists of the available material is beset by differences of opinion. Thus, the record is relatively good for shallow-water, hard-bodied marine invertebrates, but poor for most other groups, such as plants in moist tropical uplands.

Two relevant points appear to be well substantiated. First, *taxonomic diversity,* as measured by the number of recognized phyla of organisms, was greater in Cambrian times than in any later period. Second, it appears that *species diversity* and the number of families have undergone a net increase between the Cambrian and Pleistocene epochs, although interrupted by isolated phases of mass extinction (few of which are reflected in the fossil record of plants).

### B. Changes in Space

Species diversity in natural habitats is high in warm areas and decreases with increasing latitude and altitude; additionally, terrestrial diversity is usually higher in areas of high rainfall and lower in drier areas. The richest areas are tropical moist forest and, if current estimates of the number of microfaunal species (mainly insects) of tropical moist forests are credible, then these areas, which cover perhaps 7% of the world's surface area, may well contain over 90% of all species. If the diversity of larger organisms only is considered, then coral reefs such as Bunaken (see earlier) and, for plants at least, areas with a Mediterranean climate in South Africa and Western Australia may be as diverse. Gross genetic diversity and ecosystem diversity will tend to be positively correlated with species diversity.

What are not fully understood are the reasons for the large-scale geographic variation in species diversity, and in particular for the very high species diversity of tropical moist forests. The origin of diversity through the evolution of species and the maintenance of this diversity both need more study before they are better understood. This will require consideration of the present and historic (in a geological or evolutionary sense) conditions prevailing in particular areas, principally climatic but also edaphic and topographic. Climatically benign conditions (warmth, moisture, and relative aseasonality) over long periods of time appear to be particularly important.

Climax ecosystems will be more diverse than areas at earlier successional stages, but an area with a mosaic of systems at different successional stages will probably be more diverse than the same area at climax provided that each system occupies a sufficiently large area of its own. In many instances, human activities artificially maintain ecosystems at lower successional stages. In areas that have been under human influence for extended periods, notably in temperate regions, maintenance of existing levels of diversity may involve the maintenance of at least partially man-made landscapes and ecosystems, mixed with adequately sized areas of natural climax ecosystems.

## VIII. LOSS OF BIODIVERSITY AND CAUSES

Species extinction is a natural process that occurs without the intervention of humans since, over geological time, all species have a finite span of existence. Extinctions caused directly or indirectly by humans are occurring at a rate that far exceeds any reasonable estimates of background extinction rates, and to the extent that these extinctions are correlated with habitat perturbation, they must be increasing.

Quantifying rates of species extinction is difficult and predicting future rates with precision is impossible. The documentation of definite species extinctions is only realistic under a relatively limited set of circumstances, for example, where a described species is readily visible and has a well-defined range that can be surveyed repeatedly. Unsurprisingly, most documented extinctions are of species that are easy to record and that inhabit sites that can be relatively easily inventoried. The large number of extinct species on oceanic islands is not solely an artifact of recording, because island species are generally more prone to extinction as a result of human actions.

Most global extinction rates are derived from extrapolations of measured and predicted rates of habitat loss, and estimates of species richness in different habitats. These two estimates are interpreted in the light of a principle derived from island biogeography, which states that the size of an area and of its species complement tend to have a predictable relationship. Fewer species are able to persist in a number of small habitat fragments than in the original unfragmented habitat, and this can result in the extinction of species (MacArthur and Wilson, 1967). These estimates involve large degrees of uncertainty, and predictions of current and future extinction rates should be interpreted with considerable caution. The pursuit of increased accuracy in the estimation of global extinction rates is not crucial. It is more important to recognize in general terms the extent to which populations and species that are not monitored are likely to be subject to fragmentation and extinction (Temple, 1986).

Loss of biodiversity in the form of domesticated animal breeds and plant varieties is of little significance in terms of overall global diversity, but genetic erosion in these populations is of particular human concern in so far as it has implications for food supply and the sustainability of locally adapted agricultural practices. For domesticated populations, the loss of wild relatives of crop or timber plants is of special concern for the same reason. These genetic resources may not only underlie the productivity of local agricultural systems but may also, when incorporated into breeding programs, provide the foundation of traits (disease resistance, nutritional value, hardiness, etc.) that are of global importance in intensive systems and that will assume even greater importance in the context of future climate change. Erosion of diversity in crop gene pools is difficult to demonstrate quantitatively, but can be indirectly assessed in terms of the increasing proportion of world cropland planted to high-yielding, but genetically uniform, varieties. Genetic modification of organisms, varieties, or cultivars for food production, pharmaceuticals, and other products, which has caused concern in some countries but not others, may also contribute to the loss of biodiversity.

Humans exterminate species either directly by hunting, collection, and persecution or indirectly through habitat destruction and modification. Overhunting is perhaps the most obvious direct cause of extinction in animals, but it is undoubtedly far less important than the indirect causes of habitat modification in terms of overall loss of biodiversity. Hunting selectively affects the targeted species, as well as plant and animal species whose populations are subsequently affected either negatively or positively, and so it has important implications for the management of natural resources. Genetic diversity in a hunted population is liable to decrease as a result of the same factors. The genetic diversity represented by populations of crop plants or livestock is also likely to decline as a result of mass production, for the desired economics of scale demand high levels of uniformity.

Sustained human activity will affect the relative abundance of species and in extreme cases may lead to extinction. This may result from the habitat being made unsuitable for the species (e.g., clear-felling of forests or severe pollution of rivers) or through the habitat becoming fragmented (discussed earlier). Fragmentation divides previously contiguous populations of species into small sub-populations. If these are sufficiently small, then chance processes lead to higher probabilities of extinction within a relatively short time. Major changes in natural environments are likely to occur within the next century as a result of changes in global climate and weather patterns. These will cause greatly elevated extinction rates.

## IX. MAINTAINING BIODIVERSITY

### A. *In Situ* Conservation

The maintenance of biological diversity is the sustainable management of viable populations of species or populations *in situ* or *ex situ*. The maintenance of a significant proportion of the world's biological diversity only appears feasible by maintaining organisms in their wild state and within their existing range. This allows for continuing adaptation of wild populations by natural evolutionary processes and, in principle, for current utilization practices to continue. For such maintenance to succeed, it almost invariably requires enhanced management through the integrated, community-based conservation of protected areas.

Over the last thirty years, conservation biologists have struggled with the concept of the maintenance of biodiversity in highly diverse environments like rain forests. Analytical techniques (neural-net models) that allow us to reconstruct past distributions of forest types present an opportunity to predict past contractions and expansions of forest forms, and the likelihood of refugia surviving climate change. Such extrapolations must be treated with caution, as pollen samples from Brazil (for example) disproved modeling predictions that savanna grasslands should have been extant, when in fact tropical and temperate forests were present. Various authors also opposed the Pleistocene refugia hypothesis (Haffer, 1969) for the Amazon region because some evidence demonstrated the lack of rain forest fragmentation during that era. In the biogeographical zones of the Australian wet tropics, there is a strong correlation between diversity patterns and reputed rain forest refugia in both species and genetic diversity. However, this appears to have been caused by differential extinction rates in differently sized refugia rather than by allopatric speciation in the Pleistocene. Others have emphasized that a greater concentration on the Pliocene or before would be useful, since most tropical species radiations occurred before the Pleistocene.

The local-determination hypothesis of species diversity (Rosenzweig, 1995), which predicts similar species diversity in similar habitats, has also been challenged. In sister taxa of plants, the net diversification was significantly higher in Asia than in North America for genera shared between the two continents. Greater insights into the effects of current ecology on the local diversity of an area may be assisted by considering the relative ages of clades, which could establish species proliferation rates between regions, thus advancing the local versus regional diversity debate (Ricklefs and Schluter, 1993). They also tested the taxon cycle theory (Wilson, 1961) using phylogenies of bird species and showed that older species' lineages had more restricted ranges, smaller habitat breadth, and more fragmented distributions, and were closer to extinction than younger species.

In efforts to conserve biodiversity, preserving genetic dissimilarity is often a higher priority than maintaining genes of considerable similarity. Recent work shows that genetic divergence in mammals increases from the headwaters to the mouth as a river gets broader and thus becomes a greater barrier to populations on opposite banks; this effect promotes species diversity through allopatric speciation. Headwater species are basal in the phylogeny, and shared haplotypes occur only at the headwaters; this research is a contribution to Wallace's riverine diversification hypothesis in the Amazon basin.

A central question in the design of effective conservation programs is what geographical regions to protect in order to maintain the most biological diversity. The term biodiversity hotspot was coined by Myers (Myers, 1990) and most commonly refers to regions of high species richness. GAP analysis is used to identify gaps in existing protected area networks (Scott *et al.*, 1993); it uses algorithms to select the minimum set of grid cells that encompass the unprotected species. Rarity and endemicity have been used to define hotspots in bird conservation (Balmford and Long, 1994), and species richness and endemism have been used to rank countries (McNeely *et al.*, 1990). Hotspots are also defined as those areas with the greatest number of threatened species.

In setting conservation priorities, assumptions are made that indicator groups (e.g., macro-organisms such as birds, mammals, and plants) are good predictors of biological diversity in general. Another question that arises is how best to analyze biodiversity information to generate accurate and useful analyses that will inform conservation decisions. On a large scale, some concordance is found between bird diversity across continents with insect diversity (Pearson and Cassola, 1992), and in endemism patterns across taxa (Lawton, 1994); but at a finer spatial scale this correlation begins to break down. Richness in genera and families are good predictors of species richness at a finer level (Balmford *et al.*, 1996a, 1996b). However, species richness is not a good measure with which to identify hotspots for conservation because it overlooks rare species, although as the sample area for hotspots is increased, more rare species are included as a simple function of arithmetic progression. Rarity and endemicity are efficient indices for selecting the most parsimonious number of sites, but compared to complementarity measures they are less useful in defining conservation priorities.

A good conservation measure is complementarity, where the species complement of a reserve or area is identified and then further sites are found that add the greatest number of new species; this is akin to the portfolio approach (Swingland, 1997). Another method using integer linear programming to choose the optimal set of sites (maximal-covering-location; Church *et al.*, 1996) is limited to small datasets and does not achieve the greatest conservation gain for the fewest additional sites. Clearly, combining an ecosystem portfolio approach with a richness or endemism assessment would be effective, but differing approaches are needed according to the conservation goal and data availability.

### B. *Ex Situ* Conservation

Viable populations of many organisms can be maintained in cultivation or in captivity. Plants may also be maintained in seed banks and germplasm collections; similar techniques are under development for animals (storage of embryos, eggs, and sperm, i.e., "frozen zoos") but are more problematic. *Ex situ* conservation is extremely costly in the case of most animals, and while it would in principle be possible to conserve a very large proportion of higher plants *ex situ,* this would be feasible for only a small percentage of the world's organisms. Furthermore, it often involves a loss of genetic diversity through founder effects and the high probability of inbreeding (Milner-Gulland and Mace, 1998).

## X. CONTEXTUAL VARIATIONS OF THE DEFINITION

### A. Derivation of "Biodiversity"

The definition of biodiversity put forth by the Office of Technology Assessment (1987) appears to be the most widely cited basis for other published definitions

(Scott *et al.,* 1995). However, the OTA did not explain why they defined the term as they did, nor did they cite any supportive documentation. One problem with relying solely on authoritative sources for definitions of biodiversity is that different authorities have defined the term in fundamentally different ways.

"Bio" is derived from the Greek word *bios,* meaning life. Biological and biotic are terms that refer to life, living organisms, assemblages of living organisms, and the activities and interactions of living organisms. The scope of the term biological can be further understood in the context of components and processes that are considered biological. Defining biodiversity (i.e., diversity) is more difficult because it continues to be defined in several fundamentally different ways. In definitions of biodiversity, diversity has been characterized as (1) the number of different types of items, (2) the number of different types of items and their relative abundance, and (3) variety. Characterization of diversity in discussions of biodiversity has also included the structural complexity of landscapes (Huston, 1994).

## B. Classifying Biodiversity

The classification of biodiversity can be divided into those authors who consider biodiversity to be a state and those who believe that it is a measure of the state.

Most authors have defined biodiversity as a state or attribute, for example, "biodiversity is the variety of. . ." or "variety and variability of. . ." (Noss and Cooperrider, 1994). Standard dictionaries have classified diversity as a state, condition, or quality (Soukhanov *et al.,* 1988).

Other definitions of biodiversity limited the scope of the attribute to explicit, quantifiable dimensions or measures, for example, "biodiversity is the number of. . ." or "the number and relative abundance of. . ." (Office of Technology Assessment, 1987). This emphasis on quantitative, operational definitions of biodiversity and criticisms of non-quantitative definitions (Angermeier, 1994; Hunter, 1996) may signal a potential shift in the classification of the term from an attribute to a measure of an attribute. In the ecological and natural resource management literature, Pielou (1977) and others have treated diversity as a one- or two-dimensional attribute of a community (e.g., diversity is "the number of" or "the number and relative abundance of"). More recently, it has been defined as a measure or index of those attributes; for example, diversity is a "measure of. . ." (Noss and Cooperrider, 1994). Operational definitions of biodiversity (Angermeier, 1994) provide impetus to define biodiversity in quantitative terms as Hunter (1996) recommended.

## C. Attributes of Biodiversity

Another way of delineating the meaning of a term is to list its characteristics, properties, qualities, and parts. Noss (1990) recognized three main attributes of biodiversity: composition, structure, and function.

Composition addresses the identity and richness of biotic components, and the relative amount (e.g., abundance, cover, biomass) of each (Noss, 1990). Biotic components of ecosystems include genes, organisms, family units, populations, age classes, species and other taxonomic categories, trophic levels of animals (e.g., herbivores, predators), animal guilds and assemblages, plant communities, and interacting assemblages of plants, animals, and microorganisms (i.e., biotic communities).

Structural attributes of biodiversity refer to the various vertical and horizontal components of a community or landscape (Noss, 1990) and the organizational levels of plant and animal populations and assemblages (Gaston and Spicer, 1998; Hunter, 1996). Considering only biotic, vegetative components of a landscape, horizontal structure consists of the size, shape, and spatial arrangement and juxtaposition of different plant communities; vertical structure consists of the foliage density and height of different vegetation layers (Noss, 1990). Structure can also refer to population, age and trophic structure, and other levels of community organization (Hunter, 1996).

The inclusion of structure in the meaning of biodiversity provides linkages with other concepts, such as habitat diversity and the plant community concept, for both of which vegetation structure is an important differentiating attribute. Structure may have been left out of most definitions of biodiversity because the concept of biodiversity evolved from the concept of ecological diversity, which primarily focused on species diversity (Fisher *et al.,* 1943). Interestingly, 20 years ago it was asserted that measurements of diversity should not preclude structural diversity even though the term is most often used in reference to species diversity. Diversity can also be used in reference to niche width and the structural complexity of habitats.

Biotic functions represent the third component of biodiversity, and these include processes such as herbivory, predation, parasitism, mortality, production, vegetative succession, nutrient cycling and energy flow through biotic communities, colonization and extinction, genetic drift, and mutation (Noss, 1990). Biotic processes can be addressed in terms of the identity and number of different types of processes, as well as the rate (e.g., predation rate) at which each process operates.

Diversity of biotic components and processes can be observed at many biogeographic scales, from microsites and larger-scale landscape elements (e.g., vegetation types, habitat types, range sites) to regional landscapes, biomes, continents, hemispheres, and the entire biosphere (Noss, 1990; Huston, 1994; Hunter, 1996). Although these are scales at which biodiversity can be observed, they are not necessarily scales of biodiversity because most include abiotic (e.g., geological) features. Biodiversity can also be observed at several organism-based scales, including individual organisms, populations, species, and assemblages (e.g., guilds and plant communities), which themselves can be observed at various biogeographical scales.

## D. Biological Resource Asset and Management Objectives

The contextual variations in the definition of biodiversity depend on what use is being made of the biological resource asset (or bioasset), and thus the asset management objective. Biological resource values consist of direct use, indirect use, and option and non-use values. For the purposes of assessing potential use, they can be further classified as follows:

- Direct use values of *major extractive products.* Principally, this would include forestry for timber and commercial fisheries in the case of terrestrial and marine systems. Extraction of these products often involves substantial investment in capital equipment by large non-local firms, and the products are transported and sold in well-developed markets far from their original source.
- Direct use values of *"minor" extractive products.* These are naturally or semi-naturally occurring products that require labor-intensive gathering or harvesting activities, often carried out by local people. Examples include rattan, fuelwood, seaweed, wild foods, artisanal fisheries, aquarium fish, and medicinal herbs. These may be collected for sale, barter, or home consumption.
- Direct use values that require the extraction of only a small amount of biological material for *ex situ research* or storage. This includes extraction of material for biological inventories, germplasm banks, and industrial research. Extraction is often accomplished during short or long expeditions that traverse large areas to collect representative samples of biological material.
- Direct use values that are *non-extractive,* but often require considerable on-site interaction of the user with the resource. This includes ecotourism, recreation, on-site research, and other major "non-consumptive" activities occurring principally in protected areas. These activities are characterized by the need to provide food, lodging, and transport to the participants.
- Indirect use values that accrue *on site.* The primary feature of these values is that they support or protect the basic functioning of the protected area. Examples include nutrient cycling, stabilization of soils in erosion-prone areas, coastal zone stabilization, and biological support to local ecosystems. As a result of their nature, the value of these on-site functions is likely to be a component of all the other direct and non-use values generated by the area.
- Indirect use values that accrue *off site.* The value of these functions—such as watershed protection, natural ecosystems protected as national parks in generating income from wildlife tourism, protection of fisheries' nurseries and subsistence fisheries, and climate regulation—may be very large or very small depending on their relative importance to the support or protection of off-site economic activity.
- Option values. Because option values may be associated with each and every use value, they are considered only where they may be of potential significance in conjunction with the particular type of product or service.
- Nonuse values. By their very nature these values occur at a distance from the resource and require no extraction or physical interaction with the resource, for example, stewardship, ethics, cultural belief, and aesthetics.

These foregoing values are only indirectly related to biological diversity. That is, a certain level of species richness is required for these functions but there is not necessarily a direct correlation between the value of the ecosystem and its diversity. Thus, mangrove ecosystems are generally of far lower diversity than adjacent lowland terrestrial forests, but in resource terms they are likely to be of comparable value. The savannas of eastern and southern Africa, which are of great importance in generating revenues from tourism, are less diverse than the moist forests in these countries, which have far less potential for tourism.

### E. *Cave Canem* or the Precautionary Principle

At present, humans actively exploit a relatively small proportion of the world's biological diversity. Many other potential, yet undiscovered, optional and non-use values of biodiversity exist. These factors support a precautionary approach to maintaining biological diversity. In this case, the precautionary principle argues that actions should be taken to prevent further loss of biodiversity and potentially irreversible consequences *before* all biological uncertainties are resolved. Yet in conserving biodiversity, there must come a point at which the projected costs required to protect and maintain it will outweigh any probable benefits.

If species are to be viewed as a resource, and their maintenance is to be cost-effective, conservation should concentrate on systems and areas rich in species, and on those species known to be useful, or regarded as having a high probability of being useful. Thus biodiversity and its conservation would be defined purely along operational or cost–benefit lines. This bioasset perspective on biodiversity would therefore rest upon economic arguments more than biological ones.

Biodiversity has been identified as important for ecosystem health, medicinal values, agricultural purposes, and aesthetic and recreational values (Noss and Cooperrider, 1994). Noss (1990) characterized an operational definition as one that is responsive to real-life management and regulatory questions, adding that such a definition is unlikely to be found for biodiversity. Angermeier (1994) referred to an operational definition in a similar way, and Hunter (1996) suggested that a quantitative definition is needed for monitoring biodiversity and developing management plans. On the other hand, some writers assert that the confounding of definition and application is partly to blame for the confusion over how biodiversity concepts can be practically implemented.

## XI. IMPLICATIONS OF VARIATIONS IN THE DEFINITION

The need for an unequivocal and precise meaning of biodiversity that is scientifically sensible and universally applicable is imperative to help guide the design of policy and programs for the future, as well as to make critical decisions in the present. Currently, such a definition does not exist. As a concept, biodiversity is both ubiquitous and useful, particular and confusing; and for this reason it is constantly redefined on nearly every occasion.

One of the many reasons for this state of affairs is that the definition of biodiversity affects objectives in national and regional research and conservation management, and in international funding priorities. One could easily promote a timber extraction or non-timber forest product program that conserves species richness (i.e., numbers of species) at the expense of genetic diversity. Indeed, a current research program to stimulate or increase the range of tropical tree species not currently in trade, as a way to take the pressure off over-exploited species, may be misguided. It may lead to increased genetic as well as species impoverishment when foresters expand the number of species they take and select only the best and most mature specimens, thus removing the most productive and healthiest genetic stock.

Apart from the principal definitions of biodiversity discussed earlier, such as the highest number of species (i.e., species richness) and the highest level of species endemicity (Myers, 1990) or taxal endemicity (called critical faunas analysis), interpretations of pure or applied definitions are becoming more common within the vocabulary of conservation and biodiversity utilization when determining biodiversity management priorities. Some examples are national biodiversity programs that maintain "biodiversity portfolios"; biodiversity defined as flagship or keystone species diversity; viability modeling (population viability analysis) defining the species' populations to be prioritized; population analysis defining sustainability and thus defining a species' status; projects that focus on the feasibility of integrating the targeted species, assemblages, or ecosystems with the needs of local human populations and sustainable use; and (lastly) political exigency (Swingland, 1997). Although the conservation policy of a country may be driven by more pressing needs—family planning, education, politics, internal conflict, financial planning and investment, individual vested interests—current policy and decisions are also being made on the foregoing biodiversity bases rather than along strict academic lines.

Endemicity and species richness are useful starting points in defining priorities on the global level, but without information on the possibility of extinction using viability modeling or population analysis, the urgency of a given conservation action cannot be assessed. Moreover, with the increasing emphasis on the integration of local people into conservation programs to minimize long-term costs and to provide a more stable basis for the people and their natural environment, the potential for community-based conservation, coupled with sustainable use, cannot be ignored. Since national or external funding will generally provide essential support for most projects, the ecological importance of an area relative to others using an ecosystem diversity (or portfolio) approach will be a major selection criterion. The presence of a flagship or keystone species will also be significant in raising such funds. Clearly political exigencies or pure chance can enter the situation, and scientists have yet to articulate whether genetic diversity should be used as the key measure. In the absence of realistic methods of quantifying these biodiversity characteristics, they must remain imponderable objectives for the moment.

The differing approaches being advocated for biodiversity conservation are not just guided by the available methodologies but are also symptomatic of the underlying philosophies. The evolution-based approach is predominantly the preserve of biologists, and it is concerned with the maintenance of diversity as an unqualified objective unaffected by economics. The need for conservation and the uses of biodiversity—the resource-based argument—are what are used to "sell" the proposition to decision makers and policy-makers. Where these factors come together, the ideal of ecological sustainability and the conservation methods of achieving it will be possible. Because so much is now formally invested in using the word biodiversity, its definition will continue to play a crucial role in both conservation planning and public policy.

## See Also the Following Articles

BIODIVERSITY, ORIGIN OF • ECOLOGY, CONCEPT AND THEORIES OF • ECOSYSTEM, CONCEPT OF • GENETIC DIVERSITY • HABITAT AND NICHE, CONCEPT OF • LOSS OF BIODIVERSITY, OVERVIEW • MEASUREMENT AND ANALYSIS OF BIODIVERSITY • TAXONOMY, METHODS OF

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